

Bottom-up limitation of a stream salamander in a detritus-based food web

Brent R. Johnson and J. Bruce Wallace

Abstract: The indirect effects that resources can have on higher trophic levels remain poorly understood for detritus-based ecosystems. Our objective was to examine effects of long-term terrestrial litter exclusion on a larval salamander, *Eurycea wilderae*, in a detritus-based stream. After 4 years of exclusion treatment, we conducted a mark-recapture study and analyzed gut contents of *E. wilderae* larvae in the litter exclusion reach, a reach downstream of treatment, and in a reference stream. *Eurycea wilderae* growth rate (per day), density (individuals per square metre), biomass (milligrams ash-free dry mass per square metre), and production (milligrams ash-free dry mass per square metre per year) were all significantly reduced in the litter exclusion reach. Reduced density in the treatment reach was likely due to elevated hatchling drift driven by reduced prey availability. Larvae from the treatment reach had fewer prey items per gut than larvae in the reference stream and their diet consisted of fewer copepods but more midge larvae, nematodes, and terrestrial insects. The reach downstream of treatment was intermediate between reference and litter exclusion reaches for most measured parameters, indicating residual effects of upstream treatment. Our results provide the first comprehensive evidence of bottom-up limitation of a vertebrate predator in a detritus-based ecosystem and further demonstrate the importance of the terrestrial-aquatic linkage.

Résumé : Les effets indirects possibles des ressources sur les niveaux trophiques supérieurs restent mal compris dans les écosystèmes basés sur le détritus. Notre but est d'évaluer les effets de l'exclusion de la litière terrestre pendant une longue période sur les larves de la salamandre *Eurycea wilderae* dans un cours d'eau fonctionnant à base de détritus. Après 4 années d'exclusion de la litière, nous avons complété un inventaire par marquage et recapture et analysé les contenus stomacaux des larves d'*E. wilderae* dans la zone d'exclusion, dans une zone en aval de celle-ci et dans un cours d'eau témoin. Le taux de croissance (jour^{-1}), la densité (individus· m^{-2}), la biomasse (mg de masse sèche sans les cendres (AFDM)· m^{-2}) et la production (mg AFDM· $\text{m}^{-2}\cdot\text{an}^{-1}$) sont tous significativement réduits dans la zone d'exclusion de la litière. La densité réduite dans la zone expérimentale s'explique vraisemblablement par une dérive accrue des larves néonates causée par une réduction de la disponibilité des proies. Les larves de la zone expérimentale ont un nombre plus petit de proies par tube digestif que les larves du cours d'eau témoin et leur régime alimentaire contient moins de copépodes, mais plus de larves de chironomides, de nématodes et d'insectes terrestres. La plupart des paramètres mesurés dans la zone en aval de la zone expérimentale ont des valeurs intermédiaires entre celles de la zone d'exclusion et celles de la zone témoin, ce qui indique l'existence d'effets résiduels de l'exclusion en amont. Nos résultats apportent les premières preuves détaillées de l'existence d'une limitation ascendante d'un vertébré prédateur dans un écosystème à base de détritus et ils démontrent l'importance du lien entre les milieux terrestres et aquatiques.

[Traduit par la Rédaction]

Introduction

Detritus, consisting of nonliving organic matter and associated microbes, often serves as the major fuel driving ecosystems. Most consumers rely either directly or indirectly on detritus as a food resource (e.g., Fisher and Likens 1973;

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B.R. Johnson.^{1,2} Department of Entomology, University of Georgia, Athens, GA 30602, USA.

J.B. Wallace. Department of Entomology and Institute of Ecology, University of Georgia, Athens, GA 30602, USA.

¹Corresponding author (e-mail: johnson.brent@epa.gov).

²Present address: United States Environmental Protection Agency, Ecological Exposure Research Division, 26 W. Martin Luther King Drive, Cincinnati, OH 45268, USA.

Wetzel 1995). Yet, even though as much as 70–90% of all global primary production eventually enters detrital pathways (e.g., O'Neill and Reichle 1980; Pomeroy 1991), the foundations of food web theory remain grounded in the traditional grazing food chain (e.g., Hairston et al. 1960; Oksanen et al. 1981). While numerous enrichment and limitation experiments have added to our understanding of the roles of resources and consumers in structuring grazing food webs (e.g., Power 1990; Spiller and Schoener 1990; Nakano et al. 1999), manipulative experiments in detritus-based ecosystems are rare and we therefore know less about the relative strengths of top-down and bottom-up forces in shaping these systems.

Detritus-based ecosystems are fundamentally different from grazing food chains because they are typically donor controlled with the basal resource originating from outside the system. Omnivory, multiple food web links, and low interaction strengths may also be common in detrital food webs and thus prevent the simplified cascading trophic inter-

actions inherent in traditional grazing models (Strong 1992; Polis 1994; Polis and Strong 1996). Increasing evidence suggests that all trophic levels in detritus-based ecosystems can be resource limited (Richardson 1991; Wallace et al. 1997, 1999), but few studies have focused specifically on bottom-up effects of detritus on higher trophic levels (but see Polis and Hurd 1995; Chen and Wise 1999).

In a long-term ecosystem experiment, Wallace et al. (1997, 1999) reported that detritus exclusion dramatically altered benthic community structure and resulted in the lowest secondary production reported for streams. They also found that detritus limitation reduced abundance, biomass, and production of larval salamanders, the top predators in high-gradient southern Appalachian streams. The adverse effect of the exclusion treatment on predators may be significant because stream predators can be heavily subsidized from outside the system and thus rely less on in-stream resources (Mason and MacDonald 1982; Nakano et al. 1999). The studies of Wallace et al. (1997, 1999), however, combined all salamander species rather than considering responses of individual populations and were based on benthic core samples that may not accurately assess larval salamanders owing to their mobility. Additionally, the mechanisms underlying the reductions in larval salamander populations remain unclear. Reduced abundance may be due to excessive drift of larvae from the study reach, reduced adult oviposition, or increased mortality, whereas lower secondary production can be due to reduced abundance, biomass, or individual growth rate (Benke 1984).

The purpose of this study was to comprehensively examine the effects of long-term detritus reduction on the dominant salamander *Eurycea wilderae* (Blue Ridge two-lined salamander). Our specific objectives were to assess the effects of detritus limitation on *E. wilderae* population density, biomass, individual growth rate, movement, and secondary production using a mark and recapture design. Mark-recapture studies provide more accurate information about populations than benthic sampling or mesocosm studies because they can focus on responses of free-ranging individuals over the duration of the larval period. We also analyzed *E. wilderae* diets to describe potential mechanisms underlying any population differences.

Eurycea wilderae larvae are the most abundant larvae in southern Appalachian headwaters (Bruce 1985). The larval stage lasts 1 or 2 years with hatching and metamorphosis of older larvae occurring in spring and early summer (Bruce 1982, 1988; Lughart 1991). Larvae of these species are restricted to the stream where they feed on a wide variety of aquatic invertebrates (Caldwell and Houtcooper 1973; Burton 1976; Lughart 1991).

Study sites and litter manipulation

This study was conducted in two perennial first-order streams at the Coweeta Hydrologic Laboratory (US Forest Service) in Macon County, North Carolina. Coweeta is a 1625-ha drainage basin in the Blue Ridge Province of the southern Appalachian Mountains. The streams are characteristic of headwaters in the region and drain forested catchments dominated by mixed hardwoods, including oaks (*Quercus* spp.), hickories (*Carya* spp.), and yellow poplar (*Liriodendron tulipifera*). Dense growths of rhododendron

Table 1. Physical parameters of streams draining C53 (reference), C55 (litter exclusion treatment), and C56 (downstream of treatment) at the Coweeta Hydrologic Laboratory.

Variable	C53	C55	C56
Catchment area (ha)	5.2	7.5	9.9
Elevation (m above sea level)	829	810	785
Channel length (m)	100	170	65
Wetted width (m)	0.7–1.2	1.2–1.6	1.2–1.6
Average discharge ($L \cdot s^{-1}$)*	1.85	2.39	2.07
Annual average temperature ($^{\circ}C$)†	12.2	12.2	—
Annual degree-days†	4485	4512	—
Bedrock outcrop (% composition)	27	13	30
Mixed substrates (% composition)	73	87	70

Note: Elevations were measured at the gauging flumes. Wetted widths were measured during dry and wet periods. Temperature and annual degree-days were not measured for C56 and were assumed to be similar to those in C55.

*C53, 12-year average (1984–1996); C55, 5-year average (1992–1997); C56, 4-year average (1992–1996).

†C53 and C55, 12-year average (1985–1997).

(*Rhododendron maximum*) shade the streams throughout the year and limit primary production. Detailed descriptions of the Coweeta basin are given in Swank and Crossley (1988).

The study streams drain catchments C53 (reference), C55 (litter exclusion), and C56 (downstream of exclusion treatment). A 100-m reach in C53 served as a reference to examine treatment effects. Leaf litter inputs were excluded from the first 170 m of the treatment stream reach (C55) with an overhead net canopy (2.5-cm mesh) beginning in August 1993. Riparian vegetation was left intact during canopy installation to prevent changing the natural light regime. Plastic lateral drift fences (20 cm high with 1-cm mesh) were placed along each side of the treatment reach to prevent lateral inputs of terrestrial detritus or coarse particulate organic matter. Litter was removed from the canopy once each week in autumn and when needed in other seasons. Small woody debris (<10 cm in diameter) was removed from the treatment reach in summer 1996 followed by removal of large woody debris (>10 cm in diameter) in summer 1999. As a result of these manipulations, organic matter standing crop in the treatment reach has now been reduced by approximately 95% compared with pretreatment and with the reference stream (Wallace et al. 1999). A third reach, C56, extends 65 m immediately downstream of the litter exclusion treatment, so this catchment includes that of the treatment reach (C55). This reach was included to assess how the *E. wilderae* population responds to upstream detritus exclusion. The three stream reaches compared in this study have similar physical characteristics, including catchment size, discharge, and thermal regime (Table 1).

Methods

The entire wetted areas of the three study reaches (reference, treatment, and downstream of treatment) were sampled for larval salamanders approximately every month from November 1997 through April 1999. Flagging tape was placed at 5-m intervals throughout each reach to determine capture location. Stream reaches were sampled at night, when sala-

mander larvae are most active, using a small aquarium dip net (1-mm mesh) and headlamp. Owing to several ongoing studies in these streams, only loose cover objects (e.g., cobble, wood, and leaves) were turned over when searching for larvae to minimize stream disturbance. Captured larvae were placed in individual 20-mL plastic vials filled with stream water. Vials were labeled with the point of capture to the nearest 1 m and placed in a cooler.

In the on-site laboratory, each larva was anesthetized in Petri dishes containing 0.1% tricaine methanesulfonate (MS 222) (Beachy 1994). Snout–vent length was measured from the tip of the snout to the posterior vent margin to the nearest 0.5 mm using a dissecting microscope (12 \times magnification) and vernier calipers. Anesthetized larvae were then given unique marks by injecting different colors of acrylic polymers (Liquitex® brand; Binney and Smith Inc., Easton, Pennsylvania) under the skin of the tail immediately behind the hind legs (Cecil and Just 1978; Johnson and Wallace 2002). This marking procedure has proven to be an effective method for long-term marking of larval *E. wilderae* and has no adverse effects on growth or survival (Johnson and Wallace 2002). After marking, larvae were revived in stream water and released at the point of capture the following morning or evening.

Mark–recapture data were used to generate monthly population size estimates for each stream reach using the Jolly–Seber full model (Jolly 1965; Seber 1965) included in the software package POPAN-5 (Arnason et al. 1998). The Jolly–Seber model is an open population model and therefore offers greater biological realism than closed models because it allows for additions and losses within the population during the study period. Monthly population size estimates were converted to density (individuals per square metre) by dividing by mean wetted area of the study reaches over the sampling period.

We measured larval growth by two independent methods. (i) We first compared mean biomass of all larvae collected on each sample date after hatchlings appeared in May 1998. Biomass was calculated by converting snout–vent length to ash-free dry mass (AFDM) using the length–weight regression derived for *E. wilderae* in undisturbed Coweeta streams:

$$M = 0.0023L^{3.09}$$

where M is larval mass (milligrams AFDM) and L is length (millimetres) (Lughart 1991). (ii) Larval growth rates were also calculated using mark–recapture data for the entire study period. Daily growth rates (g) were calculated for all recaptured larvae as follows:

$$g = (\ln M_f - \ln M_i)/t$$

where M_i is initial larval mass (AFDM), M_f is final larval mass (AFDM), and t is the time interval between captures in days (Romanovsky and Polischuk 1982). Only initial and final masses were used for those larvae that were recaptured on multiple sample dates.

Eurycea wilderae production was calculated for the 1998–1999 cohort using the instantaneous growth method (Waters 1977; Benke 1984). Individual growth and density estimates were based on mark–recapture results, whereas biomass

(milligrams AFDM per square metre) was obtained by multiplying the population density estimate for each sample date by the mean mass of all larvae actually captured in the stream on the same date. Mean biomass, mean daily growth rate, and time interval in the sample period were multiplied to calculate interval production. Interval production estimates were then summed to get annual production (milligrams AFDM per square metre per year), which was also habitat weighted (Lughart and Wallace 1992) to account for the fact that larvae were not found on bedrock outcrops.

Larval *E. wilderae* were not collected for diet analysis until the mark–recapture study was completed in litter exclusion and downstream reaches. Approximately five larvae of the same cohort were collected seasonally from each stream reach beginning 21 July 1999 (summer). Other collection dates were 22 October 1999 (autumn), 12 February 2000 (winter), and 23 May 2000 (spring). Seasonal samples were subsequently combined in each stream to increase statistical power for comparisons among reaches. Larvae were collected at night and immediately placed in vials of Kahle's solution. In the laboratory, guts were removed under a dissecting microscope and their contents teased out and mounted on a slide with CMC-10 (Masters Company, Inc., Bensenville, Illinois). Insect taxa were identified to genus when possible except for chironomids, which were identified as either non-Tanypodinae or Tanypodinae. Noninsect taxa were identified to order. All prey items were measured to the nearest millimetre using an ocular micrometer. Prey biomass (AFDM) was then estimated using established length–mass or head width – mass regressions (Sample et al. 1993; Benke et al. 1999).

Percent similarities (Whittaker 1975) of larval diets were calculated because they provide a simple diet comparison among streams. However, statistical differences among stream reaches were assessed using the multiresponse permutational procedure (MRPP). MRPP is a nonparametric multivariate test that has proven useful in comparing species composition data (Biondini et al. 1985; Zimmerman et al. 1985).

Ecosystem-level experiments have an advantage over studies conducted on smaller scales because they more accurately account for environmental complexity and therefore have a level of biological realism that cannot be obtained from cage or mesocosm experiments (Carpenter et al. 1995; Schindler 1998). This is especially true for studies dealing with predators because enclosures can inhibit movement, provide unnatural prey densities (Cooper et al. 1990), and alter competitive interactions. Unfortunately, reduced statistical power is often the trade-off for realism in ecosystem studies (Hurlbert 1984; Carpenter et al. 1989; Schindler 1998).

Because we lacked the appropriate replication required for most statistical tests, we compared stream reaches in most cases by using bootstrapped 95% confidence intervals (CIs) (Efron and Tibshirani 1993). Data sets were bootstrapped by random resampling with replacement until 1000 data sets were produced. These recombined data sets were used to produce vectors of 1000 estimates for each parameter. The mean and approximate 95% CIs were then calculated for each vector of estimates. If the estimates followed a normal distribution, normal 95% CIs were used. However, if the vector of estimates did not follow a normal distribution, we ordered the estimates and used the 25th and 97.5th estimates

Table 2. Larval *Eurycea wilderae* captured from reference (C53), downstream of treatment (C56), and treatment (C55) streams at the Coweeta Hydrologic Laboratory from November 1997 to April 1999.

	C53	C56	C55	Total
Total individuals captured	412	323	283	1018
Total no. of recaptures	122	104	99	325
No. of larvae recaptured on multiple dates	99	70	60	229
Percent recapture	29.6	32.2	35	31.9

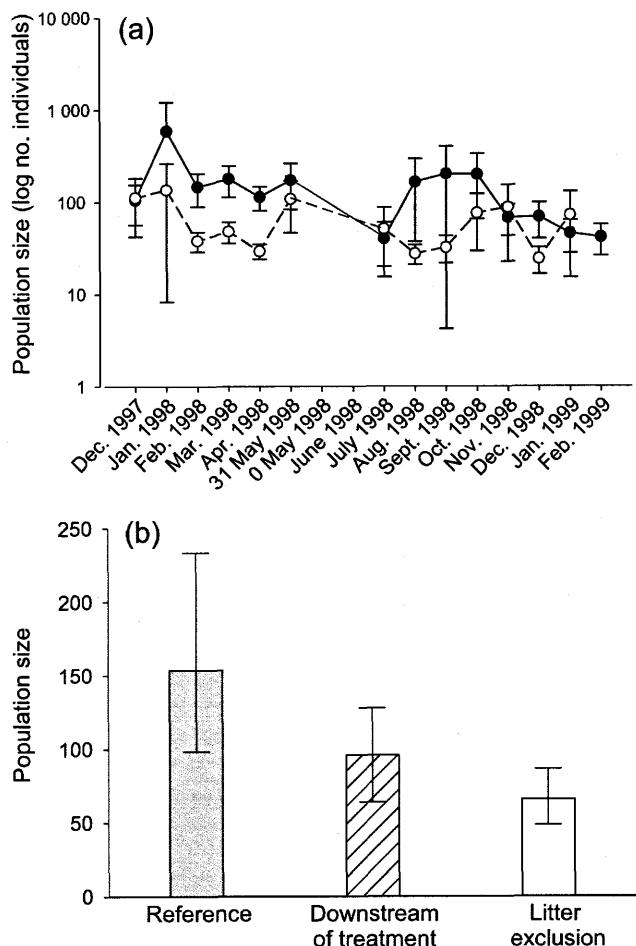
as the 95% interval boundaries (Blank et al. 1999). This often results in CIs that are not symmetrical around the mean, but the intervals accurately represent variation in the data. Errors associated with annual secondary production estimates were calculated by bootstrapping all parameters for each sampling interval (individual growth rate, biomass, and time) (Morin et al. 1987; Huryn 1996, 1998). Differences between mean values were considered significant ($p < 0.05$) when 95% bootstrapped CIs did not overlap, a conservative test for differences (Zar 1996). This method of comparison, however, prevents us from definitively stating that any differences between streams are due to treatment effects alone (Hurlbert 1984).

Results

A total of 1018 *E. wilderae* larvae were captured in the three stream reaches during the study period. Larvae were recaptured up to 10 months after initial marking, a period covering the majority of the larval stage for most individuals (Bruce 1988; Lugthart 1991). The reference stream had the highest number of both initial captures and subsequent recaptures, while the litter exclusion stream yielded the fewest (Table 2) despite the fact that it has the largest wetted area of the three streams (Table 1). Recapture rate was approximately 30% in each stream.

The litter exclusion stream had the lowest population size and density of the three study stream reaches. On nine of the 13 sampling dates, population size was greater in the reference stream than in the litter exclusion reach, while the reach downstream of treatment was typically intermediate (Fig. 1a, downstream reach omitted for clarity). On certain dates, recapture frequency was not sufficient to generate standard errors associated with population size estimates, and therefore, these dates were excluded from analyses ($n = 2$ for reference and downstream reaches, $n = 3$ for litter exclusion reach). The reference stream reach had a significantly larger mean population size over the study period (153 (98–233, 95% CI)) than the litter exclusion reach (65 (48–86, 95% CI)), whereas that of the reach downstream of treatment was intermediate (96 (± 32 , 95% CI)) and not significantly different from that of either the reference or litter exclusion reaches (Fig. 1b). Differences between stream reaches were even more apparent when population size estimates were converted to densities (individuals per square metre) to account for differences in stream size. Monthly larval densities in the litter exclusion reach remained well below those of reference and downstream reaches throughout the study period (Fig. 2a), and mean larval density in

Fig. 1. Larval *Eurycea wilderae* population sizes in reference, downstream of treatment, and litter exclusion reaches from December 1997 to February 1999. (a) log monthly Jolly–Seber population size estimates for reference (solid circles and solid line) and litter exclusion (open circles and broken line) reaches (downstream of treatment reach omitted for clarity). Values are estimates ± 1 SE (error bars). (b) Mean population size estimates per stream reach. Values are mean $\pm 95\%$ bootstrapped CI (error bars).

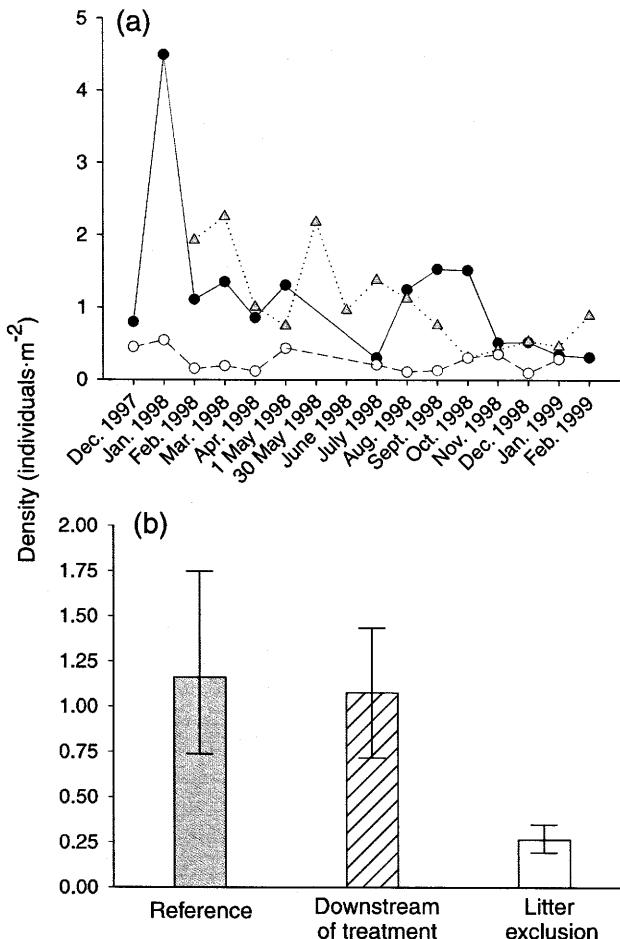


both reference ($1.16 \cdot m^{-2}$ (0.74–1.75, 95% CI)) and downstream reaches ($1.08 \cdot m^{-2}$ (± 0.36 , 95% CI)) was significantly greater than larval density in the litter exclusion reach ($0.26 \cdot m^{-2}$ (0.19–0.35, 95% CI)) (Fig. 2b).

Plots of mean biomass for the 1998–1999 cohort revealed linear growth patterns in each stream, indicating that growth was nearly continuous over the year (Fig. 3a). The slopes of the resulting significant growth rate regressions were compared among streams using analysis of covariance (ANCOVA) with time as the covariate. Regression slopes were significantly different ($p < 0.001$) among all stream reaches (reference $>$ downstream $>$ litter exclusion) (Fig. 3a).

Individual growth rates of all recaptured larvae were compared together over the study period because there was little evidence of seasonal influence on growth rate (Fig. 3a). Mean daily growth rates based on recaptured salamanders

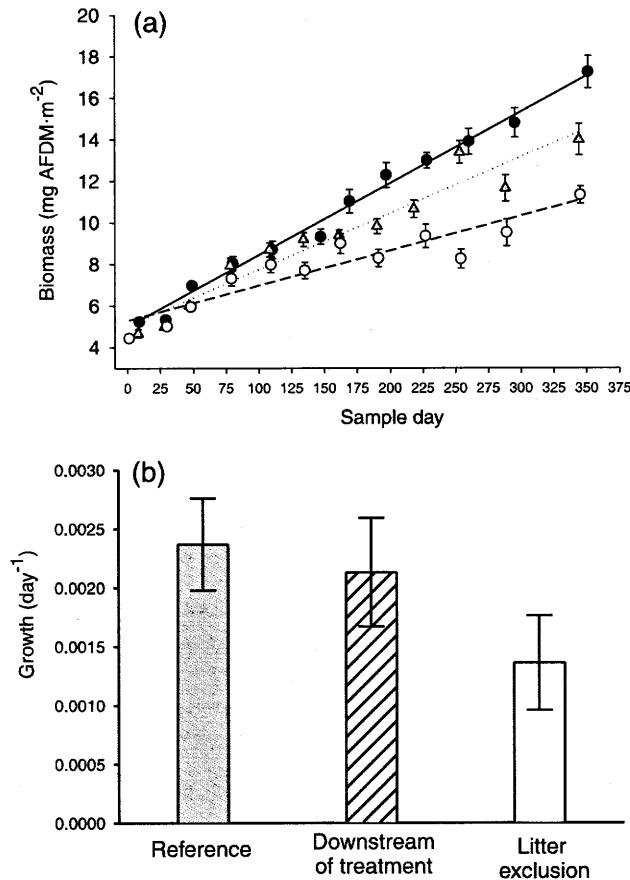
Fig. 2. (a) Monthly and (b) mean larval *Eurycea wilderae* density estimates in reference (solid circles and solid line), downstream of treatment (shaded triangles and dotted line), and litter exclusion (open circles and broken line) reaches from December 1997 to February 1999. Values are means \pm 95% bootstrapped CI (error bars).



were $0.0024 \cdot \text{day}^{-1}$ (± 0.0004 , 95% CI), $0.0021 \cdot \text{day}^{-1}$ (± 0.0005 , 95% CI), and $0.0014 \cdot \text{day}^{-1}$ (± 0.0004 , 95% CI) for the reference, downstream of treatment, and litter exclusion reaches, respectively (Fig. 3b). By this method based on recaptured larvae, growth rate differences between the reference and litter exclusion reaches was significant, while those of downstream reach was not significantly different from either.

Mean annual biomass in the reference and downstream reaches were $7.87 \text{ mg AFDM} \cdot \text{m}^{-2}$ (± 0.19 , 95% CI) and $6.62 \text{ mg AFDM} \cdot \text{m}^{-2}$ (± 0.15 , 95% CI), respectively. These estimates were greater than three times higher than that of the litter exclusion reach ($1.96 \text{ mg AFDM} \cdot \text{m}^{-2}$ (± 0.07 , 95% CI)) (Fig. 4a). *Eurycea wilderae* production was $8.50 \text{ mg AFDM} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$ (± 1.25 , 95% CI), $7.35 \text{ mg AFDM} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$ (± 1.44 , 95% CI), and $1.27 \text{ mg AFDM} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$ (± 0.33 , 95% CI) in reference, downstream, and litter exclusion reaches, respectively (Fig. 4b). Production in the litter exclusion reach was therefore approximately one fifth that of reference and downstream reaches. Annual production to

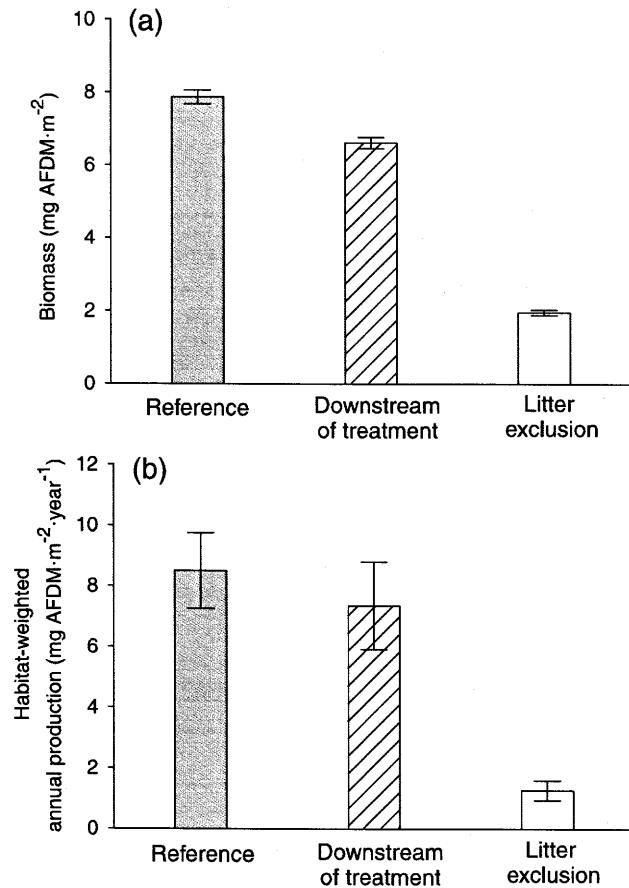
Fig. 3. (a) Relationship between time and *Eurycea wilderae* posthatching growth for the 1998–1999 cohort in reference (solid circles and solid line, $y = 0.034x + 4.991$), downstream of treatment (shaded triangles and dotted line, $y = 0.027x + 5.026$), and litter exclusion (open circles and broken line, $y = 0.017x + 5.288$) reaches. Regressions are based on mean biomass of all larvae collected on each sample date (day 0 = 1 May 1998 to day 351 = 19 February 1999). Values are means \pm 1 SE (error bars). (b) Mean individual daily growth rates of all recaptured larvae in reference ($n = 122$), downstream of treatment ($n = 104$), and litter exclusion ($n = 99$) reaches. Values are means \pm 95% bootstrapped CI (error bars).



biomass (*P/B*) turnover ratios, which provide another measure of growth, were also significantly higher in the reference (1.1 (± 0.13 , 95% CI)) and downstream (1.1 (± 0.22 , 95% CI)) reaches than in the litter exclusion reach (0.65 (± 0.17 , 95% CI))).

Sixty *E. wilderae* larvae were collected for dietary analysis (reference, $n = 18$; downstream of treatment, $n = 23$; litter exclusion, $n = 19$), and a total of 34 prey taxa were identified in the stomachs. Diets of larvae in the reference reach showed little similarity to larval diets in either the downstream (68%) or the litter exclusion (53.1%) reach. MRPP analysis further showed that larval dietary composition in the reference reach was significantly different from both downstream ($p < 0.01$) and litter exclusion ($p < 0.001$) reaches. Diets of larvae in litter exclusion and downstream

Fig. 4. (a) Mean annual biomass and (b) habitat-weighted annual production for the 1998–1999 larval *Eurycea wilderae* cohort in reference, downstream of treatment, and litter exclusion stream reaches. Values are means \pm 95% bootstrapped CI (error bars).



reaches showed the highest similarity (78.6%) and were not significantly different ($p = 0.135$) based on MRPP analysis.

The 34 prey taxa were placed into 14 major categories for comparison among reaches (Table 3). Larvae in the reference reach had significantly more total prey items per gut (22.6 (16.78–29.28, 95% CI)) than larvae in the litter exclusion reach (11.95 (9.05–14.58, 95% CI)) (Fig. 5a). The reach downstream of treatment was intermediate in prey abundance (17.53 (14.43–21.17, 95% CI)) and was not significantly different from either of the other stream reaches. Copepods and non-Tanypodinae chironomids together accounted for an average of 77.1% of all prey items in *E. wilderae* diets in the three study reaches (Table 3). Larvae in the litter exclusion reach, however, ate fewer copepods and cladocerans and significantly more non-Tanypodinae chironomids, nematodes, and terrestrial insects than larvae in the reference reach (Table 3). Differences in total prey abundance between reaches were primarily due to the large number of copepods consumed by larvae in the reference reach.

There was no difference in total prey biomass per gut among reaches (reference, 0.28 mg (0.15–0.45, 95% CI); downstream, 0.55 mg (0.37–0.77, 95% CI); litter exclusion, 0.28 mg (0.18–0.39, 95% CI)) (Fig. 5b). Non-Tanypodinae

Table 3. Bootstrapped abundance (no.gut⁻¹), biomass (mg AFDM.gut⁻¹), and percentages for prey items (no. of prey.gut⁻¹ and mass of prey.gut⁻¹) in the diets of *Eurycea wilderae* larvae from reference (REF), downstream of treatment (DWN), and litter exclusion (LE) streams.

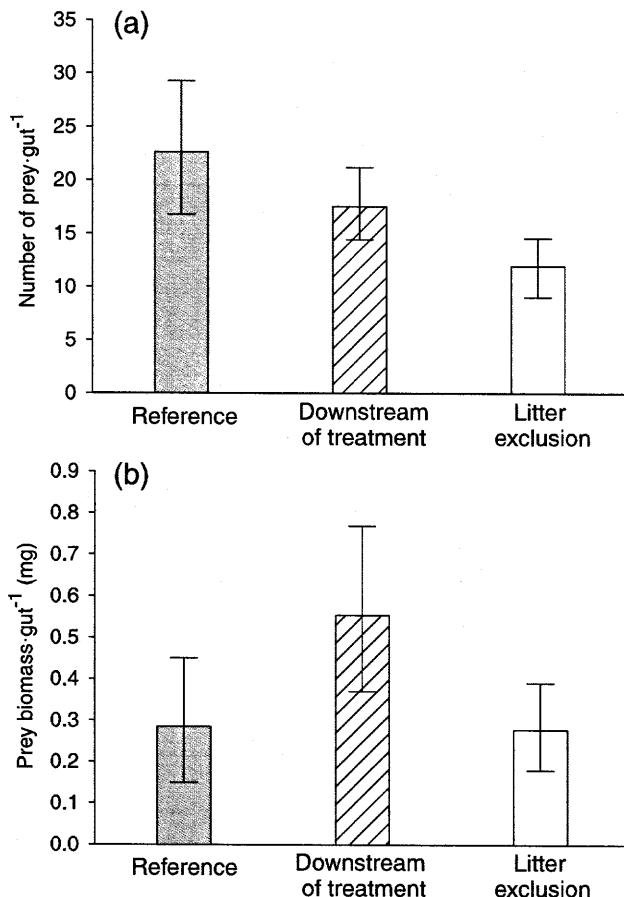
Prey category	Abundance			Biomass			Percent abundance			Percent biomass		
	REF	DWN	LE	REF	DWN	LE	REF	DWN	LE	REF	DWN	LE
Chironomidae*	5.1	7.39	6.25	0.063	0.106	0.247a	42.07ab	49.01b	30.80	30.26	35.5B	52.86
Copepoda	14.37a	6.17b	2.8b	0.015A	0.006B	0.003B	59.49a	34.51b	21.30b	14.06A	1.45A	1.60B
Cladocera	0.54a	0.04ab	0b	0.001A	0B	0.52a	0.31ab	0b	0.10AB	0A	0.06A	0B
Nematoda	0a	0.22b	0.42b	0	0.001	0.009	0a	0.47ab	3.98b	0A	0.06A	2.85B
Terrestrials	0.06	0.13	0.47	0.001	0.007	0.005	0.09a	0.88a	5.80b	0.21A	0.87AB	3.83B
Other†	2.36	3.39	2	0.1974	0.442	0.155	13.53	21.91	19.59	53.2	64.78	38.47

Note: Significant differences are indicated by letters. Values within a prey category that are followed by the same lowercase letter (abundance columns) or uppercase letter (weight columns) are not significantly different based on overlap of bootstrapped 95% CIs.

*Non-Tanypodinae chironomids.

†Includes Ephemeroptera, Plecoptera, Trichoptera, Tanypodinae, Coleoptera, Ostracoda, Acarina, Oligochaeta, and other Diptera.

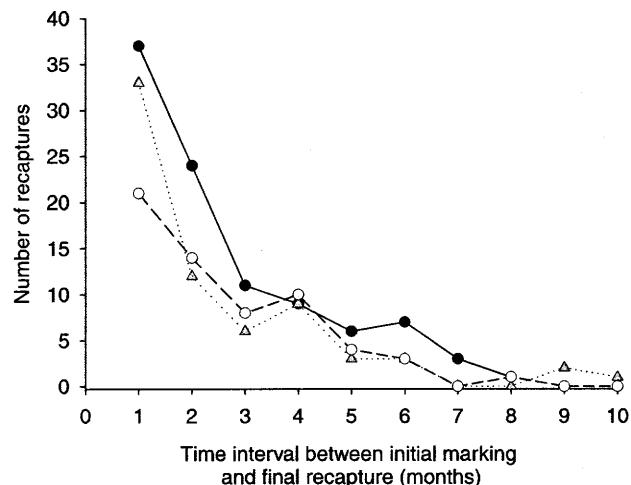
Fig. 5. (a) Total number of prey items and (b) total prey biomass per gut for larval *Eurycea wilderae* in reference ($n = 18$), downstream of treatment ($n = 23$), and litter exclusion ($n = 19$) stream reaches. Values are means \pm 95% bootstrapped CI (error bars).



chironomids alone accounted for nearly a third of total prey biomass in reference and downstream reaches and more than half of prey biomass in the litter exclusion reach (Table 3). Larvae from the reference reach had greater biomass attributed to copepods and cladocerans, whereas litter exclusion larvae had significantly higher nematode and terrestrial insect biomass in guts. Mean prey biomass was slightly higher in the downstream reach owing to the presence of a few large stonefly larvae.

Mean movements for all recaptured larvae over the study period in reference, downstream, and litter exclusion reaches were only 2.38 m (1.24–3.75, 95% CI), 2.61 m (1.41–4.14, 95% CI), and 3.37 m (0.91–6.45, 95% CI), respectively, and there was no difference among reaches. This comparison is conservative, since the litter exclusion reach is the longest of the three reaches and the chance of capturing individuals that moved longer distances was therefore greater. Only 35.7% ($n = 116$) of recaptured larvae moved ≥ 1 m, and of those that moved, the majority (65.5%) moved in the downstream direction. No larva moved > 3 m upstream (mean = 1.25 m), while the greatest downstream movement was 93 m (mean = 11.04 m). In addition, only two recap-

Fig. 6. Time interval between initial marking and final recapture for all *Eurycea wilderae* larvae recaptured in reference (solid circles and solid line, $n = 122$), downstream of treatment (shaded triangles and dotted line, $n = 104$), and litter exclusion (open circles and broken line, $n = 99$) reaches.



tured larvae were found to have drifted from the litter exclusion reach into the reach downstream.

We used the time interval between initial marking and final recapture for all recaptured larvae as a surrogate for larval survivorship (Johnson and Wallace 2002) (Fig. 6). In all three reaches, recapture probability declined with time. Recapture interval data were transformed ($\log x + 1$) and the resulting significant regression slopes (reference, $p < 0.001$; downstream of treatment, $p < 0.01$; litter exclusion, $p < 0.001$) were compared by ANCOVA with time as the covariate. There were no significant differences in survivorship of marked larvae among reaches (ANCOVA, $p = 0.23$).

Discussion

Eurycea wilderae density in the litter exclusion reach was <25% of reference and downstream reaches, despite having the largest wetted area. Reduced larval density in the treatment reach can result from greater mortality, emigration from the study reach, or reduced adult oviposition. Of the larvae that were captured and marked, there were no differences in survivorship among streams. Survivorship estimates resulted in typical type III survivorship curves (Deevey 1947) in all three streams. This survivorship pattern indicates high larval mortality and supports previously documented patterns for *E. wilderae* (Bruce 1988; Beachy 1997). Fewer initial captures in the litter exclusion stream combined with the lack of difference in survivorship of marked larvae suggest that lower larval density in the treatment stream is probably due to reduced oviposition or emigration of new hatchlings prior to initial marking.

Adult *Eurycea* feed primarily on terrestrial prey rather than on stream invertebrates (Burton 1976) and females typically oviposit on the underside of rocks rather than on in-stream woody debris or other organic matter (Baumann and Huels 1982; Bruce 1982). Therefore, treatment effects should have little influence on choice of oviposition sites.

Long-term treatment effects (beginning in 1993), however, may have resulted in fewer adult females returning to the stream. If adults move little and return to the same streams to oviposit, reduced oviposition could contribute to lower densities in the treatment reach. Unfortunately, little is known of adult *E. wilderae* movements and home range size.

Numerous chamber experiments have investigated the effects of predation by larger salamander species on larval *Eurycea* (e.g., Gustafson 1993; Beachy 1994, 1997). Results from these enclosure studies are equivocal and must be interpreted with caution. While it is possible that predation by larger salamanders contributed to greater hatchling mortality in the litter exclusion stream where other prey items are scarce (Wallace et al. 1997, 1999), such strong predatory interactions seem unlikely given that even larger *E. wilderae* larvae (>12 mm) are vulnerable to predation, and if these interactions were common, they likely would have contributed to reduced survivorship of marked larvae as well.

Eurycea bislineata larvae have a strong tendency to drift downstream after hatching as a dispersal mechanism (Stoneburner 1978; Bruce 1986). Monthly drift data from the study streams also show greater spring drift of hatchling *E. wilderae* from the litter exclusion reach compared with the reference stream (T. Siler and J.B. Wallace, unpublished data). Reduced larval density in the litter exclusion stream therefore appears to be the result of greater hatchling drift in spring prior to initial capture and marking. Hatchlings are restricted to feeding mostly on copepods and other meiofauna owing to their small gape. Copepods declined dramatically following initiation of treatment (Wallace et al. 1999) and their scarcity, along with lack of detritus cover objects, could provide the additional drift stimulus for hatchlings.

Even though excess drift response may explain density differences among streams, we found no differences in movement of marked larvae in the streams. Optimal foraging theory (reviewed by Stephens and Krebs 1987) predicts that predators should have higher densities (numerical response) and spend more time (area-restricted search) in prey-rich patches than in prey-poor patches. Owing to the significant reduction of benthic invertebrate prey in the litter exclusion stream (Wallace et al. 1997, 1999), we initially hypothesized that salamander larvae would likely encounter fewer prey-rich patches and move more in search of prey. However, larvae in all three streams were largely sedentary. Mean larval movement of all recaptures in the study streams was only 2–3 m and nearly 65% of all recaptures moved <1 m. The same individuals were often recaptured in the same depositional areas several months in a row. As with larval *E. bislineata* (Bruce 1986), the majority of the movements were in the downstream direction. Upstream movements were short (< 3 m) and took place primarily in larger depositional areas where stream velocity was low. Only two of 104 larvae recaptured in the reach downstream of treatment were found to have drifted out of the litter exclusion stream. This indicates that larvae that did not drift soon after hatching tended to stay in the treatment stream, but at the cost of reduced fitness.

The pattern of larval growth after hatching indicated that growth occurred throughout the year in each of the streams with little influence of temperature. This linear growth pat-

tern has been previously documented for *E. wilderae* larvae (Lughart 1991; Beachy 1997; Johnson and Wallace 2002) and our daily growth rate of 0.0024 (± 0.0004 , 95% CI) for recaptured larvae in the reference stream closely agrees with a previous study that measured larval *E. wilderae* growth in this stream and in the litter exclusion stream prior to treatment using both in-stream chambers (reference, 0.003·day⁻¹ (± 0.001 SE); pretreatment litter exclusion, 0.003·day⁻¹ (± 0.001 SE)) and biomass regressions from field studies (reference, 0.004·day⁻¹; pretreatment litter exclusion, 0.003·day⁻¹) (Lughart 1991). Even though results were similar, larval growth rates in chambers should be interpreted carefully because amphibian growth rates can be influenced by larval densities and prey availability (e.g., Petranka and Sih 1986; Walls 1998).

Two independent methods of growth measurement, both free from chamber effects, showed that litter exclusion resulted in significantly reduced *E. wilderae* growth. Hatchling biomass in May was very similar among streams, but by the following spring, larvae from the reference stream were an average of 52% larger than larvae from the treatment reach. Biomass regression slopes indicated that growth was significantly different among all three streams. Larval growth differences may have adverse consequences for *E. wilderae* population growth because larval growth can influence timing and size at metamorphosis and ultimately adult fecundity (Bruce 1982, 1988). Mortality also increases with duration of the larval stage (Bruce 1988). There were no obvious differences in timing or size at metamorphosis among streams, but sample sizes were too small for thorough analysis because collection of metamorphosing larvae was not an objective for this study.

Gut content analyses were performed after mark-recapture studies to explore the mechanism underlying reduced larval growth in the treatment stream. *Eurycea wilderae* fed predominantly on copepods and non-Tanypodinae chironomids. These two prey items accounted for >75% of all prey items in the guts in each stream. Similar findings were reported for *E. wilderae* in the study streams (Lughart 1991) and for larval *E. bislineata* in an Indiana stream (Caldwell and Houtcooper 1973). Burton (1976) found that *E. bislineata* larvae at Hubbard Brook, New Hampshire, relied heavily on chironomid larvae but consumed few copepods.

Larval diets in the litter exclusion reach showed low similarity to diets of larvae from the reference stream primarily because larvae in the treatment reach ate fewer copepods and relied more on non-Tanypodinae chironomids and other prey groups. Benthic data confirm that copepods have declined by 95% of pretreatment values as a result of litter exclusion, whereas midges remain a relatively available food source (Wallace et al. 1999). Larvae in the litter exclusion stream also consumed significantly more unusual prey items such as nematodes and terrestrial insects. Unlike some studies that have shown stream predators may rely heavily on prey from outside the system (Mason and MacDonald 1982; Nakano et al. 1999), in these streams, the terrestrial subsidy of prey was minor and apparently insufficient to support typical larval growth rates in the litter exclusion stream.

We initially hypothesized that food limitation was responsible for the reduction in *E. wilderae* growth because of the

significant reduction in available prey items in the treatment stream (Wallace et al. 1997, 1999). Prey abundance in larval diets supported that hypothesis, but there were no differences in total prey biomass among reaches. The abundance of copepods in larval diets from the reference stream contributed heavily to the overall difference in prey number among streams. The lack of biomass difference resulted from low copepod biomass along with the fact that litter exclusion larvae consumed a greater number of larger non-Tanypodinae chironomids. Given the similarity of prey biomass among streams, the mechanism responsible for reduced growth in the treatment stream must be either a difference in prey quality or a difference in energetic demands.

Copepods may provide a nutritious food source for larvae in the reference stream. Lugthart (1991) found that growth of larval *E. wilderae* actually increased significantly following insecticide application in C54 at Coweeta. Gut content analysis revealed that abundance and biomass of copepods were considerably higher, although not significantly so, in the diets of larvae from the insecticide-treated stream compared with the reference stream and pretreatment diets (Lugthart 1991). Lipid reserves are the most efficient energy source for organisms, and copepods in pelagic systems can have up to 70% of their dry mass as lipids (Sargent and Falk-Petersen 1988). However, these planktivorous copepods derive their high lipid content from high-quality algal food resources (Sargent and Falk-Petersen 1988) that are virtually absent in shaded headwater streams at Coweeta. Further studies are needed to assess lipid content and assimilation efficiencies of salamander prey.

Reduced growth of larvae in the litter exclusion stream could also result from differences in energetic demand. Several studies have demonstrated a positive relationship between activity and larval amphibian growth (e.g., Werner 1991; Maurer and Sih 1996). Few studies, however, have evaluated effects of reduced prey availability on activity levels (Maurer and Sih 1996), and studies linking increased amphibian activity with energetic costs are lacking. The fact that salamanders in the treatment stream ate more nematodes and terrestrial insects strongly suggests that they have difficulty finding their preferred prey. If larvae exert more energy in searching for prey, then they may have less energy available for growth. Maurer and Sih (1996) found that larvae of the stream salamander *Ambystoma barbouri* actually reduced activity in response to food deprivation in a laboratory experiment, but the study was conducted for only 9 days and in complete absence of food. Even though we found no movement differences among streams, we measured movement only to the nearest metre and did not measure activity rates on a daily basis. In situ measurements of assimilation and production efficiencies would be required to verify differences in energetic demand among streams.

Eurycea wilderae production in Coweeta headwaters ($\sim 8 \text{ mg AFDM} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$) is lower than that of many invertebrate groups (Wallace et al. 1999) because of their relatively low densities and slower growth rates. Yet, biomass and production were still significantly lower in the treatment stream as a result of reduced larval growth and density. The lower *P/B* turnover ratio in the litter exclusion stream is further evidence of reduced larval growth.

Wallace et al. (1999) calculated annual production values for all larval salamander species from benthic samples over the period 1992–1997 in the reference and litter exclusion streams. Their reference and pretreatment salamander production values ranged from 93 to 336 mg AFDM·m⁻²·year⁻¹, whereas production during treatment ranged only from 0 to 62 mg AFDM·m⁻²·year⁻¹. Based on these estimates, *E. wilderae* comprises only a small portion of the total production of the salamander community in Coweeta streams and most production is attributed to *Desmognathus* spp. *Desmognathus* spp. larvae were also collected and marked during this study, but recapture rates were insufficient for population analyses. It is likely, however, that larval *Desmognathus* spp. are similarly affected by the litter exclusion treatment given their functional similarity to *E. wilderae*.

Many of the parameters measured for *E. wilderae* in the reach downstream of treatment (population density, growth, biomass, production, *P/B*, and prey abundance) had values that were intermediate between those for reference and litter exclusion reaches. These findings indicate that larvae in this downstream reach are still affected by the upstream litter exclusion treatment, possibly because prey availability remains low in this reach. Benthic samples were not collected in C56, but Baer et al. (2001) found that invertebrate colonization, secondary production, and fine particulate organic matter accumulation on artificial substrates were significantly reduced in this downstream reach after initiation of upstream treatment. Export of fine particulate organic matter from the upstream litter exclusion reach also declined by more than 81% over the treatment period (Wallace et al. 1999). The fact that *E. wilderae* larvae downstream of treatment showed adverse effects provides additional evidence for the importance of the detrital subsidy and upstream–downstream connections in lotic systems (e.g., Vannote et al. 1980; Wallace et al. 1982; Baer et al. 2001).

Hunter and Price (1992) referred to the effects of resources on higher trophic levels as a “cascade up” and several examples exist for living plant-based systems (e.g., Peterson et al. 1993; Harvey et al. 1998). The role of detritus in the classical food web framework has been largely overlooked (Polis and Strong 1996; Polis et al. 1997) and few experimental studies have demonstrated indirect effects of resources on predators in detritus-based ecosystems. Chen and Wise (1999) found that detritus enhancement led to higher densities of predaceous mites in a forest floor community, and Polis and Hurd (1995) found that marine-derived detritus facilitated terrestrial spiders on oceanic islands. In this study, long-term exclusion of the detrital resource produced strong indirect effects that resulted in reduced density, growth, biomass, and production as well as an altered diet of larval *E. wilderae*, a vertebrate predator. Removal of detritus altered invertebrate community structure such that it was incapable of supporting a typical *E. wilderae* population. More specifically, the dramatic decline in copepod density following litter exclusion treatment appears to be at least partly responsible for declines in *E. wilderae* growth and density. Our results provide the first comprehensive study of bottom-up effects of detritus manipulation on a predatory vertebrate species and demonstrate how loss of the detrital subsidy can affect species occupying higher trophic levels.

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